



## Two new fossil species of soldier beetles (Coleoptera, Cantharidae, Malthininae) from Baltic amber

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### Abstract

Two new species of soldier beetles from the subfamily Malthininae—*Malthinus masoni* **sp. nov.** and *Malthodes markpankowskii* **sp. nov.**—are described from Baltic amber. Their discovery is yet more evidence of the remarkable number of Cantharidae in Europe during the Eocene. This diversity is likely the result of several forces, including the warmer climate that characterized the epoch as well as the wide variety of habitats where Baltic amber formed.

**Key words:** Eocene, paleoentomology, new taxa, *Malthinus*, *Malthodes*

### Introduction

Soldier beetles are quite diverse today, with more than 5,000 species (Bouchard *et al.* 2009) spread across the globe (Fanti & Damgaard 2018). Cantharids are found on all continents except the Antarctic, with species populating deserts, mountain areas and small islands (Konstantinov *et al.* 2009; Fanti & Damgaard 2018). They even live in colder places such as North Greenland and Northern Alaska (Böcher 1995; Matthews & Telka 1997; Fanti & Damgaard 2018). Cantharids primarily feed on arthropods, with some species supplementing their diet with pollen and nectar, making them important pollinators of flowers. The greatest diversity of species occurs in areas with higher temperatures, as well as those with a variety of habitats. Evidence indicates these conditions were present in the areas where Baltic amber formed (Sadowski 2017; Sadowski *et al.* 2017), spurring the evolution of numerous species of soldier beetles.

A subfamily of the Cantharidae, Malthininae Kiesenwetter, 1852 is subdivided into three extant tribes and one extinct tribe (Brancucci 1980; Kazantsev 2013). Following Brancucci (1980) and Brancucci & Wittmer (1984), 12 extant genera of this subfamily are known. Their primary diagnostic characters include the gular suture, the number of ventrites, pronotal sculpture and mandibles (Brancucci 1980; Kazantsev 2013; Fanti & Castiglione 2017). Hundreds of species of *Malthinus* Latreille, 1806 and *Malthodes* Kiesenwetter, 1852 have been described, with extant species living in areas across the Holarctic and some representatives in the Oriental region as well (Delkeskamp 1977; Ramsdale 2002; Kazantsev & Brancucci 2007).

Fossil representatives of the subfamily Malthininae were first cited at the generic level in the 19<sup>th</sup> century by Hope (1836), Giebel (1852) and Motschulsky (1857) from Baltic amber. (For a review, see Fanti 2017.) Four genera of the subfamily Malthininae (including *Malthinus* and *Malthodes*) and a subgenus have been found in Baltic amber (Fanti & Castiglione 2017; Fanti & Kupryjanowicz 2017; Kupryjanowicz & Fanti 2019). The subfamily also has been discovered in Cretaceous Burmese amber (Hsiao *et al.* 2016, 2021; Fanti 2021a; Li *et al.* 2022); however, no species of *Malthinus* or *Malthodes* has yet been found in this amber.

Currently, fossil species of *Malthinus* have been observed only in Baltic amber (Kuška & Kania 2010; Fanti 2017; Fanti & Damgaard 2018), while fossil species of *Malthodes* have been discovered in Baltic, Rovno and Bitterfeld ambers (Kazantsev 2010, 2021; Kazantsev & Perkovsky 2014; Fanti 2017, 2019, 2021a), and as compression fossils in Brunstatt brown coal deposits in France (Förster 1891) and the Vlădiceni deposits in Romania (Pintilioaie *et al.* 2021). Here we describe new extinct species of *Malthinus* and *Malthodes* in Baltic amber.

## Materials and methods

The amber pieces were found in a mine in the Yantarny settlement in Russia's Kaliningrad Region. Both specimens were purchased by the authors from an amber dealer on eBay and donated to the Smithsonian National Museum of Natural History in Washington, DC. The pieces were cut and polished to provide a better view of the inclusions. Photographs were taken by Marius Veta using a Canon DSLR camera and macro lenses on bellows, and assembled with Zerene Stacker software. Plates were processed using a PhotoImpact Viewer SE program. The illustration was created digitally using Adobe Procreate and Adobe Photoshop CC by Dr. Carly Tribull. The morphological terms follow Brancucci (1980) and Liberti (2011, 2015). The age and origin of Baltic amber have been summarized by Weitschat & Wichard (2010), and more recently by Bukejs *et al.* (2019). All specimens of Baltic amber are considered to date from the middle to upper Eocene.

## Systematic paleoentomology

### Family Cantharidae Imhoff, 1856

### Subfamily Malthininae Kiesenwetter, 1852

### Tribe Malthinini Kiesenwetter, 1852

### Genus *Malthinus* Latreille, 1806

### Subgenus *Malthinus* Latreille, 1806

### *Malthinus* (*Malthinus*) *masoni* M. G. PANKOWSKI & FANTI sp. nov.

(Figs. 1–2)

**Description.** Adult, winged, female defined on the basis of the short antennae and wide last sternite (not triangular shaped). Body length: 4.4 mm. Entirely dark brown-blackish without yellow spots on elytra, and with head and pronotum lighter brown and covered by black lines and marks.

Head exposed, strongly narrowed behind eyes, very strongly rugose, with deep and wide punctation and very few setae. Eyes very large, prominent, convex, rounded, inserted in the lateral-upper part of head. Mandibles falciform, elongated, thin. Maxillary palpi 4-segmented, with last palpomere globular and distally pointed. Labial palpi 3-segmented, with last palpomere globular and distally pointed. Antennae filiform, 11-segmented, short, reaching and surpassing two thirds of elytra; antennomere I elongated and nearly as long as the sum of antennomeres II and III, club-shaped; antennomere II about 1.7 times shorter than antennomere I; antennomeres III–V about 1.3 times longer than antennomere II; antennomeres VI–X subequal in length, millimetrically shorter than previous ones; antennomere XI elongated, very slightly pointed; all antennomeres covered by short setae. Pronotum as wide as long, narrower than head, rugose, surface slightly undulate and deeply impressed punctate, equipped with short setae, sides straight and strongly bordered, posterior and anterior margin straight and strongly bordered. Elytra short (revealing three abdominal segments uncovered), wider than pronotum, covered with deep punctation and some erect setae, parallel-sided, strongly rounded at apex. Hind wings slightly infusate, exceeding the elytra and covering last two abdominal segments. Legs slender, pubescent; coxae short, stout; trochanters slightly elongated with rounded apex; femora enlarged, rather straight; tibiae cylindrical and thin, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae longer than metafemora. Tarsi 5-segmented, pubescent; tarsomere I thin, elongated; tarsomere II about 1.5 times shorter than tarsomere I; tarsomere III very short, triangular-shaped; tarsomere IV strongly bilobed; tarsomere V elongated, slightly curved, slender; claws simple without tooth. Metasternum with rounded posterior margin, covered with many dispersed, very short setae and very shallow punctation. Sternites transverse and pubescent. Last tergite short, transverse, rounded apically; last sternite as wide as last tergite, rounded apically. Male unknown.

**Etymology.** Species named after Dr. R. Bryan Mason, a gifted neurosurgeon in Maryland who operated on the first author's mother and successfully removed her brain tumor.



**FIGURE 1.** *Malthinus (Malthinus) masoni* **sp. nov.** A: Holotype, habitus, dorsal view, scale bar = 1.0 mm. B: Holotype, habitus, dorsal view (detail), scale bar = 0.5 mm.

**Holotype.** Female, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History in Washington, DC, USA, under catalog No. 775570.

**Type locality.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad Region, Russia.

**Type horizon.** Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Syninclusions.** Detritus, botanical fragments, air bubbles and a few stellate hairs.

**Systematic placement.** The new, extinct species clearly belongs in the subfamily Malthininae based on its last maxillary palpomere that is globular and pointed distally. Characters including its triangular head behind the eyes, filiform antennae, long elytra and unmodified terminalia place the new species in the genus *Malthinus*.

**Differential diagnosis.** No sister group of *Malthinus masoni* **sp. nov.** has been found living in the Baltic region or Central Europe, and no other fossil species of *Malthinus* exhibits the same characters as the new species. *Malthinus masoni* **sp. nov.** differs from the fossil species *Malthinus danieli* Kuška & Kania, 2010 in its coloration: *Malthinus danieli* has a lighter pronotum with a black spot on the posterior half, and it has pale yellow-brown tibiae and dark femora (Kuška & Kania 2010). The new species also differs by its pronotum with straight sides: The pronotum is narrower anteriorly in *Malthinus danieli* (Kuška & Kania 2010). Compared to the new species described here, *Malthinus rifbjergi* Fanti & Damgaard, 2018 has a more transverse pronotum (1.5:1 vs. 1:1), as well as different lengths and slightly different shapes of its antennomeres (Fanti & Damgaard 2018). In the new species, for example, antennomeres II is shorter (in comparison to the other 10 antennomeres) and more club shaped than in *Malthinus rifbjergi*.

**Remarks.** The yellow rectangular amber piece measures approximately 27x16x5 mm and weighs 1.5 grams. The inclusion is complete and clearly visible. The amber piece has some superficial cracks.





**FIGURE 2.** *Malthinus (Malthinus) masoni* sp. nov. A: Holotype, habitus, ventral view, scale bar = 1.0 mm. B: Holotype, habitus, ventral view (detail), scale bar = 0.5 mm.

### Tribe Malthodini Böving & Craighead, 1931

#### Genus *Malthodes* Kiesenwetter, 1852

#### Subgenus *Malthodes* Kiesenwetter, 1852

*Malthodes (Malthodes) markpankowskii* M. G. PANKOWSKI & FANTI sp. nov.  
(Figs. 3–4)

**Description.** Adult, winged, male defined on the basis of the last urites strongly modified. Body length: 4.0 mm. Entirely blackish-dark brown without yellow spots on elytra.

Head exposed, wide, rounded, covered by short setae. Eyes large, very prominent, convex, rounded, inserted in the lateral-upper part of head. Mandibles falciform, elongated. Maxillary palpi 4-segmented, with last palpomere globular and distally pointed. Labial palpi 3-segmented, with last palpomere globular and distally pointed. Antennae filiform, 11-segmented, relatively short as they only reach the apex of elytra and about half of abdomen; antennomere I elongated, slightly club-shaped (enlarged from the middle to the apex); antennomere II about 2.0 times shorter than antennomere I; antennomere III about 1.1 times longer than antennomere II; antennomeres IV–IX subequal in length, longer than antennomere III; antennomere X about 1.4 times shorter than previous ones; antennomere XI elongated, rounded at apex; all antennomeres covered by several long setae. Pronotum strongly transverse (approximately one third wider than long), as wide as head, surface almost flat and barely punctate (shallow



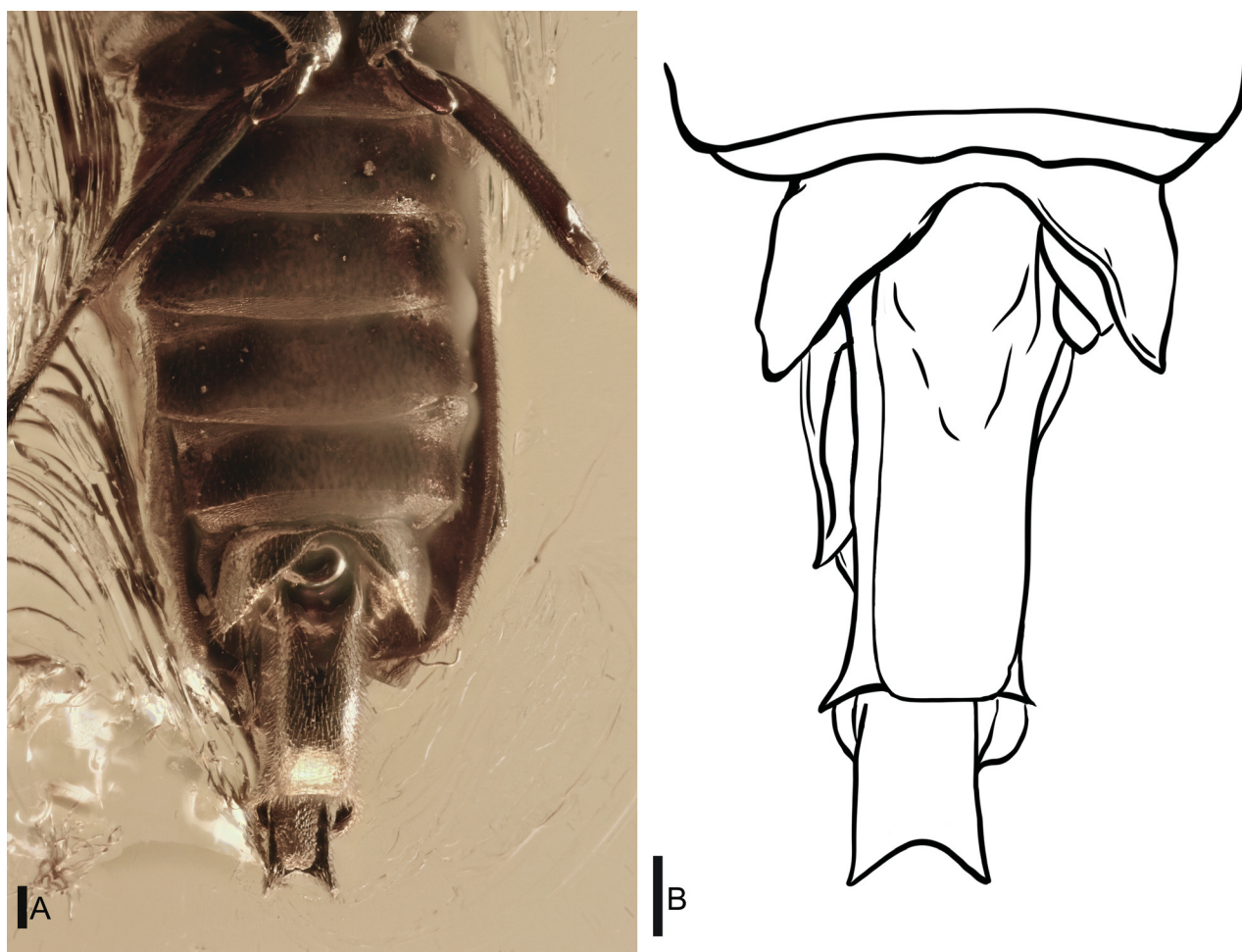
punctuation) with many short setae, sides straight and strongly bordered, posterior and anterior margin strongly bordered and very slightly enlarged/curved in the middle. Elytra short (revealing four tergites uncovered), wider than pronotum, covered with shallow punctuation and several erect setae, parallel-sided, strongly rounded at apices. Hind wings infusate, exceeding the elytra and partially covering penultimate tergite but not the last one. Legs slender, pubescent; coxae short, stout; trochanters elongated with rounded apex; femora enlarged, slightly curved; tibiae cylindrical and thin, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae as long as metafemora. Tarsi 5-segmented, pubescent; tarsomere I thin, elongated; tarsomere II shorter than tarsomere I; tarsomere III shorter than second; tarsomere IV strongly bilobed; tarsomere V elongated, slightly curved, slender; claws simple without tooth. Metasternum with rounded posterior margin, covered with many dispersed, short setae. Sternites transverse and pubescent. Penultimate tergite (tg9) wide, subrectangular; last tergite (tg10) narrower than penultimate tergite, elongated, with apical margin rather deeply concave; last sternite (st9) very elongated, as narrow as last tergite, apically almost straight (very slightly emarginate). Aedeagus not visible. Female unknown.

**Etymology.** Species named after Mark S. Pankowski, the big-hearted father of the first author.

**Holotype.** Male, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USA, under catalog No. 775571.



**FIGURE 3.** *Malthodes (Malthodes) markpankowski* sp. nov. A: Holotype, habitus, dorsal view, scale bar = 0.5 mm. B: Holotype, habitus, detail of metasternum, scale bar = 0.2 mm. C: Holotype, habitus, ventral view, scale bar = 1.0 mm. D: Holotype, habitus, ventral view (detail), scale bar = 0.5 mm.



**FIGURE 4.** *Malthodes (Malthodes) markpankowskii* sp. nov. A: Holotype, habitus, detail of last abdominal segments (ventral view), scale bar = 0.1 mm. B: Reconstruction of last abdominal segments, scale bar = 0.1 mm. Illustration by Dr. Carly Tribull.

**Type locality.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad Region, Russia.

**Type horizon.** Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Syninclusions.** Many stellate hairs, detritus, botanical fragments and air bubbles.

**Systematic placement.** This new, extinct species clearly belongs to the subfamily Malthininae based on its last maxillary palpomere that is globular and pointed distally. Its rounded head behind eyes, filiform antennae and strongly modified *terminalia* place the new species in the genus *Malthodes*.

**Differential diagnosis.** No sister group of *Malthodes markpankowskii* sp. nov. has been found living in the Baltic region or Central Europe, and no other fossil species of *Malthodes* has this combination of characters (in particular the shape of the *terminalia*) shown by *Malthodes markpankowskii* sp. nov. One fossil species that is vaguely similar is *Malthodes neumanni* Fanti, 2019 from Bitterfeld amber. It differs by the shorter last sternite (st9) with a more concave anterior margin (Fanti 2019), and by its shorter last tergite (tg10). The other slightly similar species is *Malthodes meriae* Fanti, 2018 from Baltic amber. Compared with the new species described here, *M. meriae* has a much smaller and shorter last tergite, as well as a last sternite with a more concave anterior margin (Fanti 2018).

**Remarks.** The yellow rectangular amber piece measures approximately 26x13x4 mm and weighs 1.2 grams. The inclusion is complete and clearly visible except for small areas around the head.

## Discussion

The discovery of these two new species of Cantharidae offers yet more evidence that the family was quite diverse



in Europe during the Eocene (Fanti 2017, 2021b). Many of these species were captured and preserved in Baltic amber, giving us a detailed picture of the insects living in these areas at the time. The forces that propelled this high biodiversity, as already proposed in Parisi & Fanti (2020), likely included the warmer climate of this epoch. Scientists have recognized the connection between biodiversity and warmer climates since the early 19<sup>th</sup> century (Erwin 2009). Many researchers have attempted to explain this connection, offering such hypotheses as (1) warmer climates allow more species to exploit specialized niches; (2) warmer climates promote bigger populations and thus higher resistance to extinction; and (3) warmer climates spur faster speciation and/or slower extinction rates (Erwin 2009). Furthermore, the diversity of Cantharidae was also probably due to the wide variety of habitats where Baltic amber formed, including coastal lowland swamps and angiosperm-conifer forests, which created a “heterogeneous mosaic-like landscape” in these areas (Sadowski 2017; Sadowski *et al.* 2017). The other factor that favors speciation could have been the high soil humidity present in the Eocene. As we have seen for some living species in Sardinia (Italy), certain soil and litter conditions can prevent or disrupt normal larval development (Liberti 2021), and thus reproductively isolate various populations. The resulting abundance of Cantharidae species during the Eocene makes these beetles especially interesting candidates to study. Among the easiest to distinguish are species of *Malthodes*, as males possess characters (for example, the last abdominal segments) that are easily recognized in amber inclusions. Many other genera, including those of *Malthinus*, *Cantharis* Linnaeus, 1758, *Rhagonycha* Eschscholtz, 1830 and *Podistra* Motschulsky, 1839, have much more uniform diagnostic characters and therefore are often quite difficult to describe as new species from amber. It is very probable, however, that like *Malthodes*, these genera were more diversified 40 million years ago than they are today.

## Acknowledgements

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## References

- Böcher, J. (1995) Palaeoentomology of the Kap København Formation, a Plio-Pleistocene sequence in Peary Land, North Greenland. *Meddelelser om Grønland, Geoscience*, 33, 1–82.
- Bouchard, P., Grebennikov, V.V., Smith, A.B.T. & Douglas, H. (2009) Biodiversity of Coleoptera (Chapter 11). In: Footitt, R.G. & Adler P.H. (Eds.), *Insect Biodiversity: Science and Society*. Wiley-Blackwell Publishing Ltd, Garsington Road, Oxford, 632 pp.
- Brancucci, M. (1980) Morphologie comparée, évolution et systématique des Cantharidae (Insecta: Coleoptera). *Entomologica Basiliensia*, 5, 215–388.
- Brancucci, M. & Wittmer, W. (1984) Zur Kenntnis der indomalaiischen Malthininae (Coleoptera, Cantharidae). *Entomologica Basiliensia*, 9, 183–192.
- Bukejs, A., Alekseev, V.I. & Pollock, D.A. (2019) Waidelotinae, a new subfamily of Pyrochroidae (Coleoptera: Tenebrionoidea) from Baltic amber of the Sambian peninsula and the interpretation of Sambian amber stratigraphy, age and location. *Zootaxa*, 4464 (2), 261–273.  
<https://doi.org/10.11646/zootaxa.4664.2.8>
- Delkeskamp, K. (1977) *Coleopterorum Catalogus Supplementa. Pars 16. Fasc. 1. Cantharidae*. W. Junk, The Hague, 485 pp.
- Erwin, D.H. (2009) Climate as a Driver of Evolutionary Change. *Current Biology*, 19 (14), R575–R583.  
<https://doi.org/10.1016/j.cub.2009.05.047>
- Fanti, F. (2017) Catalogo Cantharidae fossili del mondo. *Fossils & Minerals Review*, 2, 1–18 [abbreviated Italian version. Available: 12 March 2017] World catalog of fossil Cantharidae. *Fossils & Minerals Review*, 2 (Special Issue), 1–52 [extended English version. Available: 25 May 2017].
- Fanti, F. (2018) *Malthodes meriae* sp. nov.: a new fossil *Malthodes* Kiesenwetter, 1852 from the Eocene Baltic forests (Coleoptera: Cantharidae). *Studies and Reports, Taxonomical Series*, 14 (2), 243–248.
- Fanti, F. (2019) First fossil soldier beetles (Coleoptera Cantharidae) from Bitterfeld amber, Germany. *Zitteliana*, 93, 89–96.
- Fanti, F. (2021a) Two new *Malthodes* and a new *Podistra* from Eocene Baltic amber (Coleoptera, Cantharidae). *Baltic Journal of Coleopterology*, 21 (1), 1–9.
- Fanti, F. (2021b) A new genus of Cantharidae from Eocene Baltic amber found in Poland, with phoretic mites. *Baltic Journal of Coleopterology*, 21 (2), 105–110.

- Fanti, F. & Castiglione, E. (2017) Description of a new genus and species of Cantharidae from Eocene Baltic amber (Insecta, Coleoptera). *Palaeodiversity*, 10, 123–127.  
<https://doi.org/10.18476/pale.v10.a8>
- Fanti, F. & Damgaard, A.L. (2018) Fossil soldier beetles from Baltic amber of the Anders Damgaard amber collection (Coleoptera Cantharidae). *Baltic Journal of Coleopterology*, 18 (1), 1–32.
- Fanti, F. & Kupryjanowicz, J. (2017) A new soldier beetle from Eocene Baltic amber. *Acta Palaeontologica Polonica*, 62 (4), 785–788.  
<https://doi.org/10.4202/app.00388.2017>
- Förster, D.B. (1891) Die Insekten des “Plattigen Steinmergels” von Brunstatt. *Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen*, 3 (5), 335–593 + [1], 6 pls., (6) + [1].
- Giebel, C.G.A. (1852) *Deutschlands Petrefacten. Ein systematisches Verzeichniss aller in Deutschland und den angrenzenden Ländern vorkommenden Petrefacten nebst Angabe der Synonymen und Fundorte*. Abel A. Verlag, Leipzig, xiii + 706 pp.
- Hope, F.W. (1836) Observations on Succinic Insects. *The Transactions of the Entomological Society of London*, 1, 133–147.  
<https://doi.org/10.1111/j.1365-2311.1838.tb00157.x>
- Hsiao, Y., Li, Y., Ren, D. & Pang, H. (2021) Morphological phylogenetics provide new insights into the classification and evolution of fossil soldier beetles from Mid-Cretaceous Burmese amber (Coleoptera: Cantharidae). *Zoological Journal of the Linnean Society*, 193, 1271–1293.  
<https://doi.org/10.1093/zoolinnean/zlaa184>
- Hsiao, Y., Ślipiński, A., Deng, C. & Pang, H. (2016) A new genus and species of soldier beetle from Upper Cretaceous Burmese amber (Coleoptera, Cantharidae, Malthininae). *Cretaceous Research*, 69, 119–123.  
<https://doi.org/10.1016/j.cretres.2016.09.002>
- Kazantsev, S.V. (2010) New *Malthodes* (Insecta: Cantharidae: Coleoptera) from the Rovno Amber (Upper Eocene of Ukraine). *Russian Entomological Journal*, 19 (2), 105–107.  
<https://doi.org/10.15298/rusentj.19.2.02>
- Kazantsev, S.V. (2013) New taxa of Baltic amber soldier beetles (Insecta: Coleoptera: Cantharidae) with synonymic and taxonomic notes. *Russian Entomological Journal*, 22 (4), 283–291.
- Kazantsev, S.V. (2021) New species of Baltic amber soldier beetles (Insecta: Coleoptera: Cantharidae). *Russian Entomological Journal*, 30 (2), 153–158.  
<https://doi.org/10.15298/rusentj.30.2.08>
- Kazantsev, S.V. & Brancucci, M. (2007) Cantharidae. In: Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palearctic Coleoptera. Vol. 4. Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea, Cucujoidea*. Apollo Books, Stenstrup, pp. 234–298.
- Kazantsev, S.V. & Perkovsky, E.E. (2014) A new *Malthodes* and some other interesting soldier beetles (Coleoptera: Cantharidae) from Late Eocene Rovno amber. *Russian Entomological Journal*, 23 (2), 113–116.  
<https://doi.org/10.15298/rusentj.23.2.03>
- Konstantinov, A.S., Korotyaev, B.A. & Volkovitsh, M.G. (2009) Chapter 7. Insect biodiversity in the Palearctic Region. In: Footitt, R.G. & Adler, P.H. (Eds.), *Insect Biodiversity: Science and Society*. Wiley-Blackwell Publishing Ltd, Garsington Road, Oxford, pp. 141–202.  
<https://doi.org/10.1002/9781118945568.ch7>
- Kupryjanowicz, J. & Fanti, F. (2019) New subgenus and three new species of soldier beetles from the Eocene of Baltic amber. *Palaeontologia Electronica*, 22.2.22A, 1–13.  
<https://doi.org/10.26879/895>
- Kuška, A. & Kania, I. (2010) New soldier beetles (Coleoptera, Cantharidae) from the Eocene Baltic amber. *Zootaxa*, 2400 (1), 49–56.  
<https://doi.org/10.11646/zootaxa.2400.1.5>
- Li, Y.-D., Biffi, G., Kundrata, R., Huang, D.-Y. & Cai, C.-Y. (2022) *Nothotytthonyx*, a new genus of Malthininae (Coleoptera, Cantharidae) from mid-Cretaceous amber of northern Myanmar. *ZooKeys*, 1092, 19–30.  
<https://doi.org/10.3897/zookeys.1092.81701>
- Liberti, G. (2011) Le specie di *Malthodes* Kiesenwetter, 1852 delle Alpi Marittime e Liguri (Coleoptera, Cantharidae). *Annali del Museo Civico di Storia Naturale “G. Doria”*, Genova, 103, 147–246.
- Liberti, G. (2015) Le specie di *Malthodes* Kiesenwetter, 1852 d’Italia nord-occidentale (Coleoptera, Cantharidae) (*Malthodes* di Lombardia: 2° contributo alla conoscenza dei *Malthodes* italiani). *Annali del Museo Civico di Storia Naturale “G. Doria”*, Genova, 107, 1–151.
- Liberti, G. (2021) Le specie insulari di *Malthodes* Kiesenwetter, 1852. I. Arcipelago Toscano e Sardegna (Coleoptera, Cantharidae) (6° Contributo alla conoscenza del genere *Malthodes* in Italia). *Annali del Museo Civico di Storia Naturale “G. Doria”*, Genova, 113, 417–481.
- Matthews Jr., J.V. & Telka, A. (1997) Insect Fossils from the Yukon. In: Danks, H.V. & Downes, J.A. (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, pp. 911–962.
- Motschulsky, V.I. (1857) Voyages. Lettre de M. de Motschulsky à M. Ménétrés. N. 4. *Études Entomologiques*, 5, 21–38.
- Parisi, F. & Fanti, F. (2020) Baltic amber: A new *Cacomorphocerus* Schaufuss, 1892 with two specimens preserved in a single piece, and four new *Malthodes* Kiesenwetter, 1852. *Zootaxa*, 4778 (3), 546–560.  
<https://doi.org/10.11646/zootaxa.4778.3.6>



- Pintilioaie, A.-M., Fanti, F. & Ionesi, V. (2021) First finding of a fossilized Cantharidae (Insecta: Coleoptera) from the Middle Miocene deposits in Romania. *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"*, 64 (1), 73–80.  
<https://doi.org/10.3897/travaux.64.e64706>
- Ramsdale, A.S. (2002) Family 64. Cantharidae Imhoff 1856. In: Arnett, R.H. Jr., Thomas, M.C., Skelley, P.E. & Frank J.H. (Eds.), *American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, Florida, pp. 202–218.
- Sadowski, E.-M. (2017) *Towards a new picture of the "Baltic amber forest"—flora, habitat types, and palaeoecology*. Thesis, Georg-August-Universität, Göttingen, v + 119 pp.
- Sadowski, E.-M., Schmidt, A.R., Seyfullah, L.J. & Kunzmann, L. (2017) Conifers of the "Baltic amber forest" and their palaeo-ecological significance. *Stapfia*, 106, 1–73.
- Weitschat, W. & Wichard, W. (2010) Baltic amber. In: Penney, D. (Ed.), *Biodiversity of fossils in Amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 1–304.